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Fast food: the transport of particulate organic matter over an upwelling event on the west coast of southern Africa


Baboon Point, Elandsbaai – José Enrico

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ABSTRACT

Differences in transport, composition and supply of particulate organic matter (POM), as a food source for coastal consumers, were investigated between an exposed headland (Cape Columbine) and a sheltered bay (Elandsbaai) in the southern Benguela. Physical data, in agreement with previous studies, showed that Cape Columbine is situated within an upwelling center and Elandsbaai within an upwelling shadow. Three distinct oceanographic conditions, upwelling, relaxation and downwelling, were discernable from wind, current and temperature data at each site. Upwelling was most prevalent at Cape Columbine in contrast to relaxation at Elandsbaai. Significant differences ($P < 0.00001$) in chlorophyll *a* concentration, quantities of organic carbon and % kelp-derived carbon were found between the two sites. In addition, significant differences ($P < 0.0001$) in chlorophyll *a* concentration, quantities of organic carbon and % kelp-derived carbon were found between the different oceanographic conditions: upwelling, relaxation and downwelling. A significant interaction ($P < 0.00001$) for % kelp-derived carbon was found between site and oceanographic conditions. Tests within study sites revealed significantly higher chlorophyll *a* concentrations in the euphotic zone, as expected. Furthermore, chlorophyll *a* concentrations showed a significant decrease with distance offshore at Elandsbaai. Percentage contribution of kelp-derived carbon (max = 36%) to POM was lower than predicted and surprisingly lower than values reported in previous works (77%). No stratification of kelp-derived matter or organic carbon was observed in the water column at both sites. It is likely that sampling stations were too shallow i.e. water column was well mixed as a results of nearshore turbulence. In terms of food supply to coastal consumers, upwelling episodes at Cape Columbine resulted in significantly high import of kelp matter into the nearshore water column. In contrast, phytoplankton, constituted the primary food source for both sites during relaxation and downwelling episodes. It is clear that different oceanographic conditions between an exposed headland and a sheltered bay have profound implications regarding the transport, composition and supply of POM, as a source of food to coastal communities.

INTRODUCTION

The Benguela Upwelling System along the west-coast of southern Africa is regarded as one of the most intense upwelling systems in the world (Kamstra 1985, Jury 1985, Taunton-Clark 1985, Holden 1985, Branch & Branch 1988). Strong equatorward winds, underwater topography and the shape of the coastline are among the factors which result in the upwelling of nutrients to surface coastal waters (Hartline 1980, Shannon 1985, Bustamante and Branch 1996, Hill et al. 2006). Such rapid input of nutrients into the euphotic zone results in large blooms of phytoplankton upon which many consumers depend as a primary source of food (Probyn 1985, Painting et al. 1993). However, recent studies incorporating stable isotope analysis (Bustamante and Branch 1996, Kaehler et al. 2000, Kaehler et al. 2006), have shown that the diets of coastal consumers, spanning several trophic levels, are subsidized by macroalgal-derived matter. Subsequently, it has been suggested that uptake of macroalgal carbon by filter feeders, via detrital food webs in benthic and pelagic communities, has been underestimated (Bustamante and Branch 1996, Duggins and Eckman 1997). Hence the importance of phytoplankton versus macroalgal detritus as food sources for benthic communities is being increasingly called into question. Research by Mann (1988) has shown that macrophytic detritus is effectively used by coastal invertebrates, leading to increased shellfish production.

Extensive forests of the kelps *Ecklonia maxima* and *Laminaria pallida* fringe the rocky shores along the west-coast of southern Africa. On average they contribute more than 70% of all particulate organic matter (POM) while phytoplankton seldom exceeds 7%. Furthermore, Bustamante and Branch (1996) have shown that more than 50% of the carbon and 65% of the nitrogen assimilated by South African west-coast filter-feeders (*Aulacomya ater, Mytillus galloprovincialis* and *Gunnarea capensis*) can be attributed to kelp-derived detritus. Kelp beds are regarded as highly productive, exceeding phytoplankton production an estimated 2 to 3.5 times per unit area (Beckley and Branch 1992). In addition to high productivity, their broad distribution and common occurrence make kelp beds a globally important detrital food source (Duggins and Eckman 1997). Most of this production enters the detrital food web when kelp blades are eroded and fragmented by the action of waves (Newell 1984, Mann 1988).

As a non-mobile entity, POM is delivered to the intertidal zone by oceanographic processes, which are predicted to have a significant effect on the quality and quantity of POM supplied to nearshore intertidal and subtidal zones (Hill et al. 2006). Upwelling, downwelling and relaxation events, are the predominant local oceanographic processes operating along the west-coast of southern Africa, and it has been shown that are responsible for the import of nutrients upon which phytoplankton thrive (Branch and Branch 1988, Painting et al. 1993). These oceanographic processes are also likely to serve as transport mechanisms, influencing the composition and rate at which POM is transported to coastal consumers.

The most prominent coastal currents off the South African west-coast are related to upwelling cycles, which consist of episodes of active upwelling, followed by relaxation and/or down-welling events and recur every 2-10 days during summer. Upwelling is initiated by favorable alongshore winds (northward on a west-coast in the southern hemisphere) which, in conjunction with the Coriolis Effect, result in an offshore flux of surface water known as the Ekman transport (Csanady 1981, Bernard et al. 2006). For each pulsed wind event, cold, dense water is drawn to the surface from great depth and replaces the warmer less dense surface water, which moves farther offshore as upwelling progresses (Shanks et al. 2000). Subsequently, coastal waters become well-mixed, replenished with nitrogen, and can be described as cold and relatively isothermic. As this water matures, phytoplankton seed cells exploit this renewed supply of nitrogen, growing to form dense blooms (Painting et al. 1993, Hutchings 1985). At some distance offshore, a sharp boundary is formed where the upwelled water and the less-dense surface water meet; this point is known as the upwelling front (Shanks et al. 2000). As soon as the prevailing wind dies, upwelling is brought to an abrupt halt and, without additional disturbance, relaxation occurs. During this process, solar heating stabilises the water column which becomes stratified, resulting in a warm surface layer of water which overlies a cooler bottom layer. The surface layer of less-dense water moves independently over this cooler bottom layer and often washes ashore when upwelling ceases. In the event of wind reversal, downwelling occurs (Bernard et al. 2006), during which the upwelling front is pushed in a shoreward direction thereby the upwelled water in the lower reaches of the nearshore water column. With continued southward and onshore winds, it is plausible that this process may transport POM onshore. Such POM is likely to contain living phytoplankton, which naturally occurs within the surface layer of mature upwelled water (Painting et al. 1993). More importantly, however, particulate kelp-derived matter stirred up from the sea floor as a result of upwelling, probably constitutes the majority this POM – based on previous findings by Bustamante and Branch (1996). The mixture of the two yields a valuable food source that can be transported ashore under favourable oceanographic conditions and identified as a sudden, abundant boost of available food.

The west coast of South Africa can be divided into localised upwelling-centres and upwelling-shadows (Andrews and Hutchings 1980). Upwelling-centres typically occur on exposed headlands where, under the influence of equatorward winds, plumes of upwelled water originate (Painting et al. 1993). Bays and protected stretches of coastline, lying within the path of upwelling plumes, fall within what is referred to as an upwelling-shadow. On the west coast of South Africa, upwelling-shadows never experience true, intense upwelling as they are often protected from the wind and sheltered by the headlands of southward upwelling-centres (Andrews and Hutchings 1980). Such differences in coastal topography have significant effects on local oceanographic conditions, and hence supply of POM. Painting et al. (1993) have shown that mature upwelled water, characteristic of upwelling-shadows, is conducive to high levels of phytoplankton productivity in comparison to the newly upwelled water of upwelling centres. Such discontinuities along the west coast of South Africa, provide an ideal system to study transport of POM in relation to upwelling cycles and coastline topography.

Cape Columbine and Elandsbaai situated along the west-coast of southern Africa (Figure 1), display major physical and ecological differences, making them ideal locations for this investigation. Cape Columbine is an exposed headland situated within an upwelling-centre. Elandsbaai is a sheltered embayment north of Cape Columbine and lies within the upwelling-shadow. It was predicted that greater amounts of kelp would enters the detrital food web at Cape Columbine than at Elandsbaai as a result of increased abrasion associated with higher wave action and turbidity present at this exposed headland. It was thus expected that POM should contain a higher proportion of kelp-derived matter at Cape Columbine in comparison to Elandsbaai. Following upwelling events at Cape Columbine, nutrient-rich upwelled water is likely to flow northward and undergo retroflection, ending up in St. Helena Bay and Elandsbaai a few days later. This is the result of the 'sheltering effect' of Cape Columbine, which will enhance chlorophyll concentrations in mature, nutrient-rich upwelled water at St. Helena Bay and Elandsbaai, while chlorophyll *a* in the core of the upwelling plume will be held at minimal levels (van der Lingen et al. 2006). This study aims to isolate events of sudden increases in POM supply to nearshore coastal water and, in conclusion, identify those physical parameters responsible for the transport of this food source. Such findings would provide a greater understanding behind the functioning of an incredibly complex ecosystem, providing the link between abiotic factors, affecting food supply and ultimately coastal community structure.

The central objectives of this study were to answer the following questions:

1. Are there differences in amounts of POM (consisting of phytoplankton, organic carbon and kelp) between a headland and an adjacent bay?

2. How do upwelling, downwelling and relaxation episodes influence quantities of POM between a headland and an adjacent bay?

3. How is POM distributed throughout the water column and at different distances offshore on a headland and in an adjacent bay?

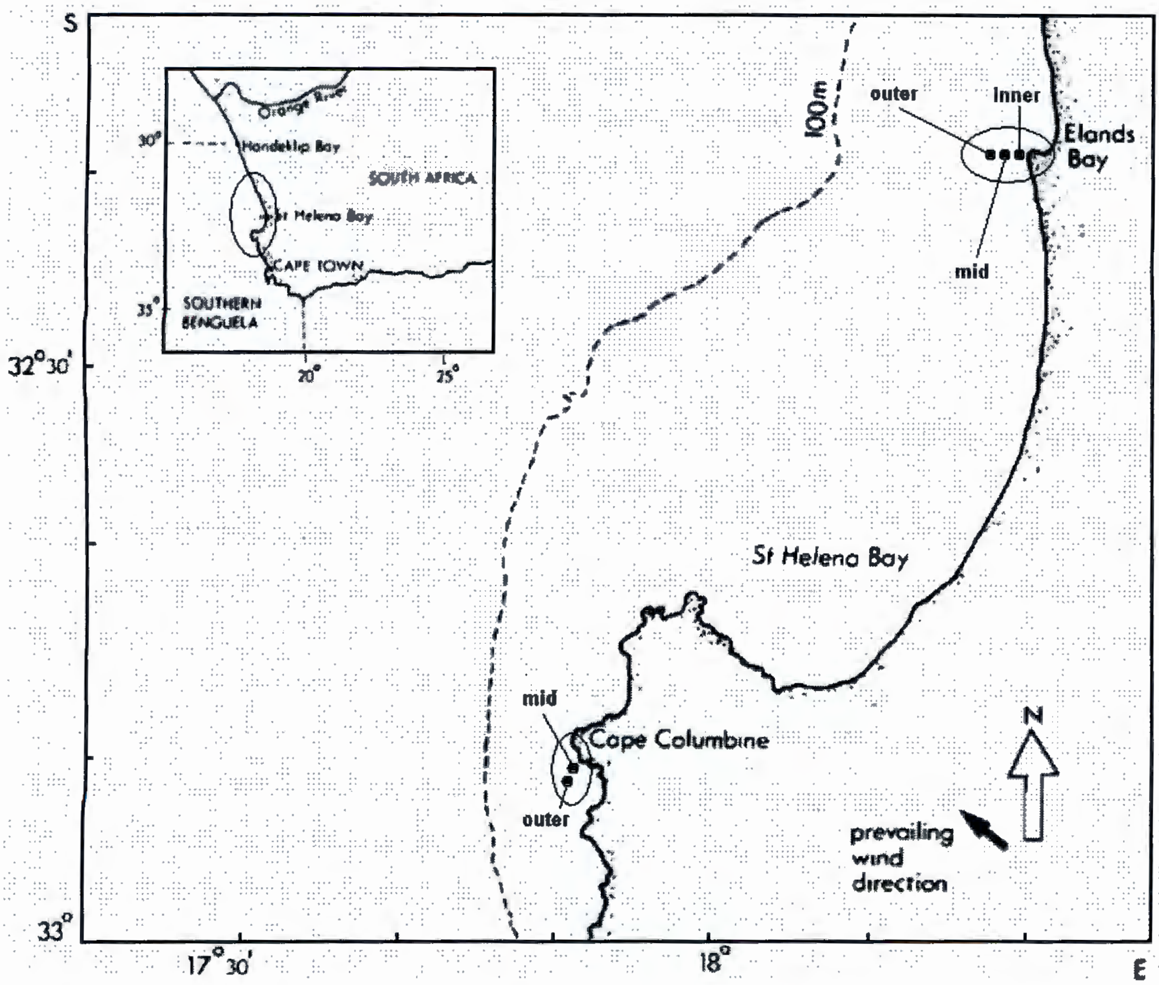

Fig. 1: Elandsbaai (sheltered – upwelling shadow) and Cape Columbine (exposed headland – upwelling center) study sites. Black dots denote sampling stations at each of the study sites and the dashed line, the 100 m isobath. Note the prevailing wind direction.

MATERIALS AND METHODS

Collection of physical data

Temperature throughout the water column was measured at each of the sites using Onset TidBit® temperature loggers programmed to record *in situ* temperature every five minutes. Loggers were placed along a moored thermistor chain at 5 m, 8 m, 12 m and 17 m depths in 20 m deep water at Elandsbaai and Cape Columbine in the vicinity of sampling stations (Figure 1). Wind direction and speed were recorded as hourly averages by a meteorological station at Elandsbaai and at 08h00, 14h00 and 20h00 by the lighthouse keepers at Cape Columbine. ADCP's (Acoustic Doppler Current Profilers) were deployed in 20 m deep water at each of the study sites in order to record current direction and velocity throughout the water column.

Collection of biological data

Sampling was conducted aboard a ski-boat during summer from 6 Jan 2007 to 6 Feb 2007 at Elandsbaai and Cape Columbine (Figure 1), alternating between sites each day. Three sampling stations were established at Elandsbaai – an "inner" station at 8 m depth (0.2 km offshore, sampled at 0, 4 and 8 m depth intervals), a mid station at 15 m depth (0.7 km offshore) (sampled at 5 m intervals) and an outer station at 20 m depth (1.4 km offshore) (sampled at 5 m intervals). Two sampling stations were established at Cape Columbine – a mid station at 20 m depth (0.7 km offshore) (sampled at 5 m intervals) and an outer station at 36 m depth (1.4 km offshore) (sampled at 6 m intervals) – (a planned inner sampling station at Cape Columbine was aborted as access was too dangerous). GPS co-ordinates for each sampling station are plotted in Figure 1. Discrete 1-*l* water samples were obtained at each depth interval using remotely triggered Niskin® bottles. Water samples were then transferred into opaque plastic bottles and immediately stored in a cooler box to limit phytoplankton production. Upon arrival at shore samples were refrigerated and processed the same night. Each water sample was halved and both halves vacuum-filtered in low-light conditions through 4.7 cm Munktell® GF/F glass microfibre filters (0.45 μm pore size). Exact volumes of water filtered through each filter paper were recorded. Filter papers were then wrapped in aluminium foil and stored at -80°C for further analysis. Two filters were thus obtained from each water sample, one for Chlorophyll-*a* analysis and the other for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis.

Chlorophyll-*a* analysis was performed using the Welschmeyer method of flourometry (Welschmeyer 1994). Pigments were extracted from filter papers in 90% acetone for 24 h and then analysed spectrophotometrically. Chlorophyll-*a* values served as an index for both photosynthetically active and non-active biomass i.e. both living and dead cells. Filter papers for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis were oven-dried at 40°C for 48 h. The mass of the filtrate from each sample could not be determined as the variance around the mass of the filter papers exceeded the actual mass of the organic filtrate itself. Therefore the topmost layer of the filter paper containing the organic matter was removed and folded into Santis tin capsules. Samples were then combusted in a flash EA 1112 series elemental analyser (Thermo Finnigan, Italy) and the gases were passed to a Delta Plus XP IRMS (isotope ratio mass spectrometer) (Thermo electron, Germany), via a Conflo III gas control unit (Thermo Finnigan, Germany). The in-house standards used were Choc, a commercial chocolate/egg mixture solid sold in the United States of America, and Merck Gel, a proteinaceous gel produced by Merck. Both Standards were calibrated against IAEA (International Atomic Energy Agency) standards. The nitrogen ratios were compared with atmospheric nitrogen, while carbon ratios were calculated relative to PDB (PeeDee Belemite). Results are expressed in standard delta notation $X = [(R_{sample} \div R_{s\tan dard}) - 1] \times 1000$, where X = the element in question and R = ratio of the heavy isotope over the light isotope.

Analysis of physical data:

Wind, daily average temperature at fixed depth intervals in the water column, and current time-series data were aligned according to dates and visually represented for each site. Elandsbaai wind data were plotted as a vector diagram, whereas the data for Cape Columbine were decomposed into along-shore and across-shore components and plotted as a line graph as only three readings (averages) were recorded each day. Daily average temperatures were represented as line graphs for each specific depth interval and current data were split into along-shore and across-shore components and plotted as a continuous variable on a colour gradient throughout the water column. Distinct oceanographic episodes of active upwelling, downwelling and relaxation were visually identified by inspecting the wind direction, temperature throughout the water column and current direction for each day.

Analysis of isotope data:

Upon weighing filter papers in the laboratory, it was discovered that the variance around the mass of the filter paper itself exceeded that of the organic material which had been deposited after filtration. Hence mass could not be used as a proxy for detecting differences in amounts of POM present in the water column. However, $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis of the filter papers yielded an integrated result measured in millivolts (area mV) which is proportional to the mass of organic material incinerated in the mass spectrometer. Given that this relationship is linear, I assumed that area mV would serve as a proxy for detecting differences in amounts of organic material throughout the water column during the study period. To test this assumption, several samples of Merck Gel ranging in mass from 0.092 mg to 0.671 mg were passed through the mass spectrometer. The relationship between mass of organic matter and the area mV output was positive and linear ($R^2 = 0.999$ for both carbon and nitrogen). Hence area mV was used as a quantitative proxy for the amount of POM deposited on filter papers.

Reference values obtained from the literature displayed a high range in $\delta^{15}N$ isotopic ratios (e.g. 4 – 8‰ for phytoplankton) whereas $\delta^{13}C$ isotopic ratios were relatively consistent. Furthermore, results showed that $\delta^{15}N$ isotopic ratios were erratic in comparison to $\delta^{13}C$ isotopic ratios. Nitrogen is often limiting in marine ecosystems, hence all available nitrogen is consumed regardless of isotope content, resulting in no overall isotope fractionation (Fry 2006). Therefore all stable isotope analyses in this study were based on $\delta^{13}C$ isotopic ratios.

The two-source mixing model was based on $\delta^{13}C$ isotopic ratios for *E. maxima* and phytoplankton: -12‰ and -20‰ respectively (Bustamante and Branch 1996). Percentage kelp-derived matter within each POM sample was determined as follows:

$\%C_{kelp\ derived} = \dfrac{(\delta^{13}C_{phytoplankton} - \delta^{13}C_{POM})}{(\delta^{13}C_{phytoplankton} - \delta^{13}C_{kelp})} \times 100$, where $\delta^{13}C_{phytoplankton}$ and $\delta^{13}C_{kelp}$ are values obtained from the literature, and $\delta^{13}C_{POM}$ is the value obtained from the mass spectrometer for a filter paper sample.

Ten blank filter papers were combusted in the mass spectrometer and average organic carbon calculated. Area C mV (referred to as organic carbon hereafter) for POM samples were corrected for the volume of water filtered and the average organic carbon value for a blank filter paper subtracted. Chlorophyll *a* and (corrected) organic carbon values for POM samples were log-transformed to meet the assumptions of a normal distribution for analysis of variance (ANOVA). Depth at each sampling station was divided into two layers (top and bottom) as follows:

Table 1: Division of water column into top and bottom depth categories for each sampling station.

Site	Station	Depth	
		Top	**Bottom**
Elandsbay	Inner	0, 4 m	8 m
	Middle	0, 5 m	10, 15 m
	Outer	0, 5 m	10, 15, 20 m
Cape Columbine	Middle	0, 5 m	10, 15, 20 m
	Outer	0, 6, 12 m	18, 24, 30, 36 m

Differences in chlorophyll *a*, organic carbon and percentage kelp-derived carbon were first compared between Cape Columbine and Elandsbay using a factorial ANOVA to analyse the higher order interactive effects of multiple categorical factors. Categorical factors used were: site (Cape Columbine/Elandsbay – fixed factor) and oceanographic conditions (i.e. upwelling/downwelling/relaxation – fixed factor). Differences in chlorophyll *a*, organic carbon and percentage kelp-derived carbon were then tested within sites using a factorial ANOVA based on fixed categorical factors: distance offshore (inner/middle/outer for Elandsbaai, and middle/outer for Cape Columbine) and depth (top/bottom). A post-hoc Tukey Honestly Significant Difference (HSD) test was performed for each ANOVA. Statistical analyses and were performed using STATISTICA® 7.0 (Statsoft, Inc. 2004). Physical and biological time-series data were plotted using MATLAB 6.5.

RESULTS

Elandsbaai - upwelling cycles

Wind, temperature and current data from Elandsbaai (Fig. 2a, b, c and d) clearly showed distinct periods of upwelling, downwelling and relaxation. On 5 Jan 2007, at the start of the study period, relaxation was taking place as the water column was well stratified with a temperature of ~11 °C at 5 m depth and ~10°C at 17 m (Fig. 2b). This is corroborated by the independent movement of the warmer surface layer of water (0 – 10 m) in relation to the cooler, denser bottom layer (10 – 20 m). The predominant current direction within the surface layer of water was northwards at moderate speed, whereas the bottom layer displayed even weaker movement in this direction and showed slight reversal tending towards a southerly direction (Fig. 2c and d). An increase in the strength of northward wind on 8 Jan 2007, initiated a well-defined episode of active upwelling, which lasted for three days and terminated on 11 Jan 2007 as a result of a brief reversal in wind direction (Fig. 2a). During this period the temperature throughout the water column was cold and isothermic with surface temperature at 5 m depth dropping to 10°C, approximately the same temperature as that at 17 m depth (Fig. 2b). As a result of the increased wind speed, the direction of the current throughout the entire water column (down to 20 m depth) was affected. The predominant direction of the current was typical to that of a classic upwelling episode, with water moving northward and westward offshore (Fig. 2c and d). The following relaxation cycle lasted for six days from 12 Jan 2007 to 18 Jan 2007, during which the water column and wind direction displayed similar properties to the first relaxation cycle. Following a period of strong northward wind on 19 Jan 2007 relaxation ceased and a brief, intense upwelling episode took place for two days. The water column and wind direction displayed similar properties to the earlier upwelling episode, but, there was no significant offshore movement of water. Upwelling ceased on 21 Jan 2007 with a reversal from northward to southward wind direction leading to a brief period of relaxation on 22 Jan 2007. Wind of a southward direction persisted for the following six days, reaching maximum speed on 27 Jan 2007 and 28 Jan 2007. This resulted in the complete reversal of currents throughout the water column, giving rise to a well developed downwelling cycle i.e. a dominant southward current. During this period, the water column was warm and stratified with elevated temperatures reaching a maximum of 17.74°C at the surface (5 m depth) and a maximum of 15.3°C

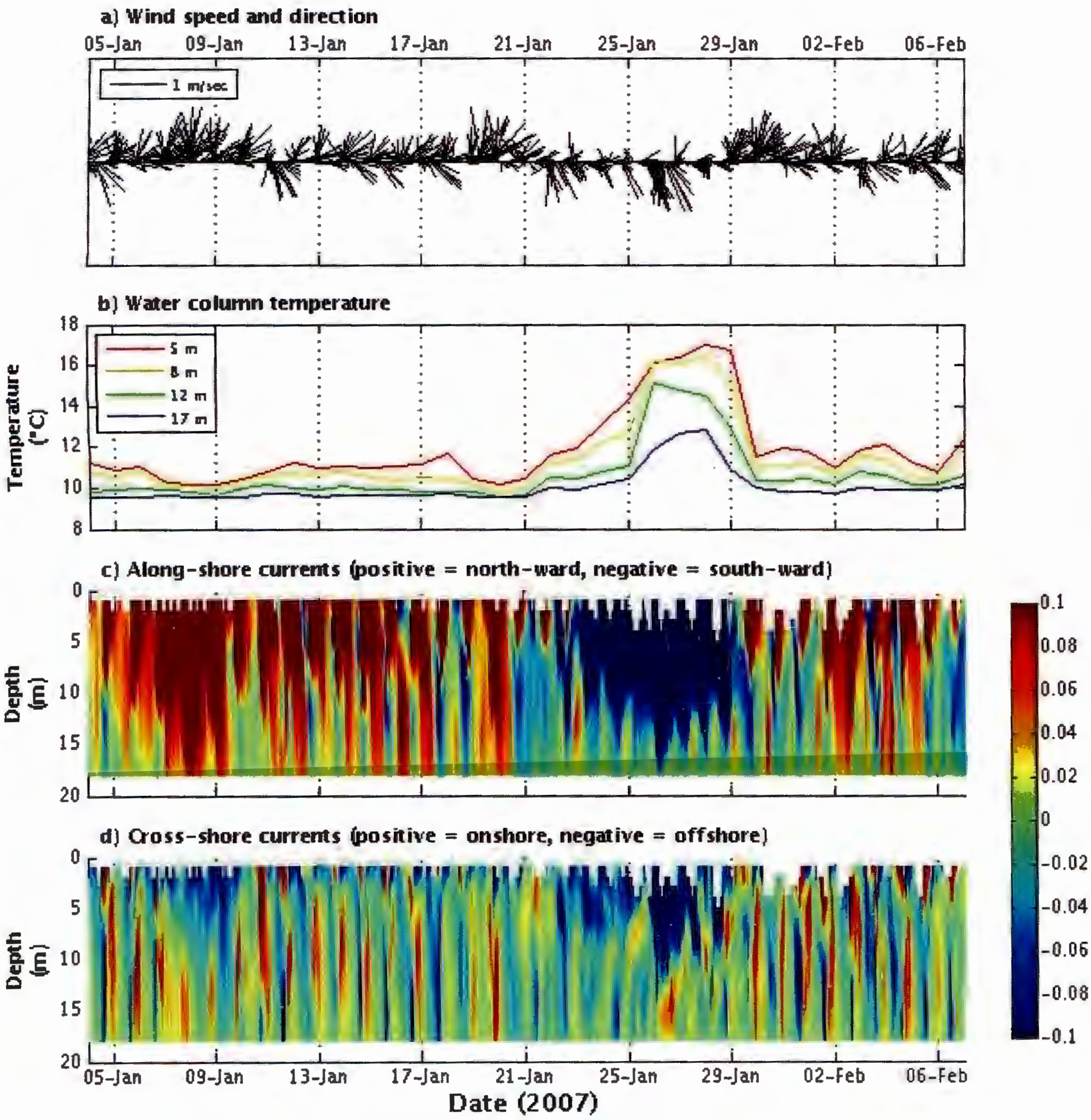

Fig. 2: Elandsbaai physical data: collected throughout the study period. (a) Wind vector diagram: vectors above the x-axis represent equatorward winds (from the south) conducive to upwelling, vectors below the x-axis represent poleward winds (from the north) conducive to downwelling (magnitude of vectors expressed in m/s). (b) Daily average temperature (°C) at specified depth intervals. (c) Along-shore currents throughout the water column: positive values (red) represent equatorward flow, negative values (blue) represent poleward flow. (d) Cross-shore currents: positive values (red) represent onshore flow, negative values (blue) represent offshore flow.

at the bottom (17 m). Wind reversal occurred on 29 Jan 2007, returning to a northward direction and thus terminating the downwelling cycle with a brief and weak upwelling event. Relaxation followed and continued until 5 Feb 2007 when sampling ended.

Elandsbaai - chlorophyll a, organic carbon and kelp-derived POM

Clear fluctuations in the amount of chlorophyll *a* and percentage of kelp-derived carbon were discernable at Elandsbaai (Fig. 3). On average, high concentrations of chlorophyll *a* were restricted to the euphotic zone, above 10 m depth. Prominent peaks in chlorophyll *a* concentration were apparent during 10 – 12 Jan 2007 followed by 15 – 18 Jan 2007, to a lesser extent, 22 – 24 Jan 2007, and finally during 1 – 5 Feb 2007 at all distances offshore (Fig. 3a, b and c). A severe drop in chlorophyll *a* was noted from 26 Jan 2007 until 31 Jan 2007.

On average, quantities of organic carbon (Fig. 3d, e and f), mirrored concentrations of chlorophyll *a*. Highest quantities of organic carbon were restricted to surface layers of water, above 5 m depth. Major peaks were detected from 16 to 18 Jan 2007 and from 1 to 3 Feb 2007. Furthermore, a mild, subsurface peak was observed from 22 Jan 2007 to 26 Jan 2007.

High percentages of kelp-derived carbon (Fig. 3g-i) were recorded at the beginning of the study period from 6 Jan 2007 to 8 Jan 2007 at all distances offshore (Fig. 3h and i). On 14 Jan 2007, approximately 75% of the carbon sampled on the surface (0 m) at the inner station, 200 m offshore, was kelp-derived (Fig. 3g). High values (> 40%) were recorded at 4 and 8 m depth. The following day of sampling (16 Jan 2007) revealed a significant reduction in kelp-derived carbon at all stations throughout the water column. On 18 – 20 Jan 2007 significant percentages (~15 – 40%) of kelp-derived carbon were only detected shallower than 10 m. The following day revealed highest percentages of kelp-derived carbon at the lowest depths: a maximum of ~70% was recorded at the bottom (15 m depth) for the middle station. Following this, a peak in % kelp-derived carbon throughout the water column at all sampling stations was recorded from 24 – 30 Jan 2007. Average values were highest at the innermost sampling station with 100% recorded at the surface on 24 Jan 2007. The very next sampling day, 26 Jan 2007, revealed 100% kelp-derived carbon at the surface for the middle sampling station. On 1 Feb 2007 and 3 Feb 2007, highest percentages of kelp-derived carbon were obtained from the greater depths. Of

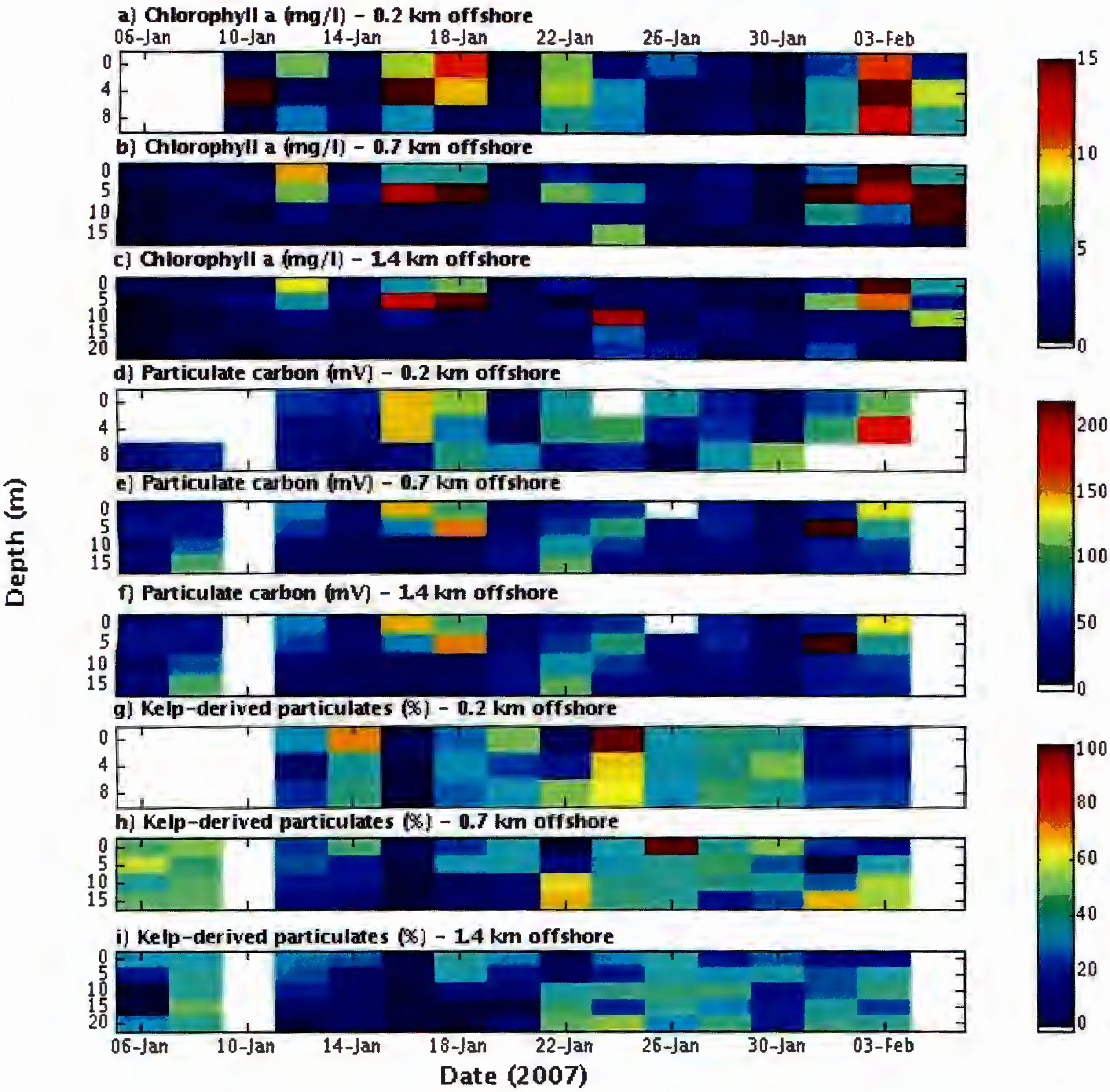

Fig. 3: Biological data for Elandsbaai: Chlorophyll *a* concentrations (mg/l) at specified depth intervals are shown for (a) the inner station, (b) the middle station and (c) the outer station. Quantity of organic carbon (mV = millivolts) is given for specified depth intervals at (d) the inner station, (e) the middle station and (f) the outer station Percentage kelp-derived carbon of particulate organic matter is given for specified depth intervals at (g) the inner station, (h) the middle station and (i) the outer station. High values are represented towards the red end of the spectrum and low values towards the blue end.

particular significance is the middle station with highest values, 60 – 70% recorded below 10m depth.

Cape Columbine - upwelling cycles

Upwelling, relaxation and downwelling events could readily be discerned (Fig. 4). During the first three days of sampling at Cape Columbine (07 – 11 Jan 2007), the daily average water temperature throughout the water column was low and isothermic reaching a minimum of 9.47°C at 5 m depth and 8.96°C at 17 m depth (Fig. 4b), suggesting the presence of an upwelling cycle. The northward wind direction (Fig. 4a) and subsequent northward and offshore current throughout the water column (Fig. 4c and d) confirmed the occurrence of an upwelling event. A decrease in northward wind speed and an increase in the onshore wind component ended the upwelling event and brought about a long period of relaxation from 13 Jan 2007 until 19 Jan 2007. The water column became well stratified and displayed physical properties similar to relaxation events recorded at Elandsbaai (Fig. 3). Water temperature increased to a maximum of 15.7°C at 5 m depth, and a maximum of 13.3°C at 17 m. On 21 Jan 2007 an upwelling event took place until 23 Jan 2007 as a result of increased northward and offshore wind speed. Minimum temperatures recorded during this event were 9.62°C and 9.27°C at 5 m and 17 m intervals respectively. Upwelling ceased on 25 Jan 2007 and downwelling commenced with reversal in wind direction to southward and onshore. Downwelling continued until 29 Jan 2007, during which the water column was isothermically warm attaining a maximum temperature of 16°C at 5 m depth and 13.6°C at 17 m depth. The wind direction returned to northwards on 31 Jan 2007, increasing in speed and terminating the downwelling event. Mild upwelling persisted until 2 Feb 2007 with the water column undergoing relaxation for the remainder of the study period.

Cape Columbine - chlorophyll a, organic carbon and kelp-derived POM

Chlorophyll *a* and the percentage of kelp-derived carbon, fluctuated at Cape Columbine (Fig. 5). Like Elandsbaai, chlorophyll *a* levels were low throughout the entire water column at all distances offshore during the initial period of the study – from 7 Jan 2007 to 11 Jan 2007 (Fig. 5a, b). An increase in chlorophyll *a* concentration was detected from 13 Jan 2007 to 19 Jan 2007 at both distances offshore. Concentrations then steadily decreased and were hardly detectable on 21 Jan

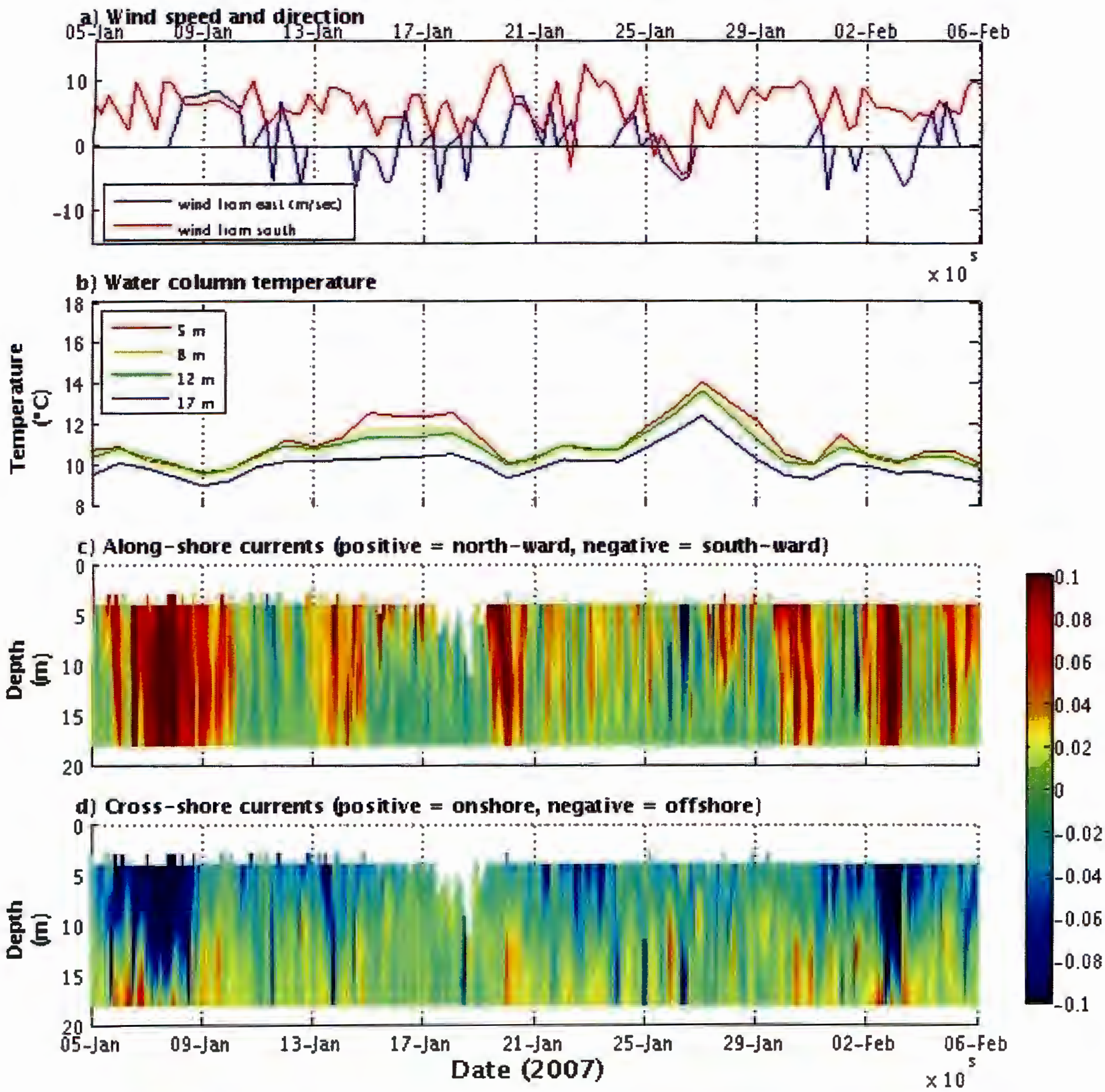

Fig. 4: Cape Columbine physical data: (a) Decomposed wind direction and speed. The red line represents the along-shore wind component: where the line is above the x-axis the wind direction is equatorward (from the south, i.e. upwelling-conducive), where the line is below the x-axis the wind direction is poleward (from the north, i.e. downwelling-conducive). The blue line represents the across-shore wind component: where the line is above the x-axis the wind direction is offshore (from the east, i.e. upwelling-conducive), where the line is below the x-axis the wind direction is onshore (from the west, i.e. downwelling-conducive). (b) Daily average temperature (°C) at specified depth intervals. (c) Along-shore currents throughout the water column: positive values (red) represent equatorward flow, negative values (blue) represent poleward flow. (d) Cross-shore currents: positive values (red) represent onshore flow, negative values (blue) represent offshore flow.

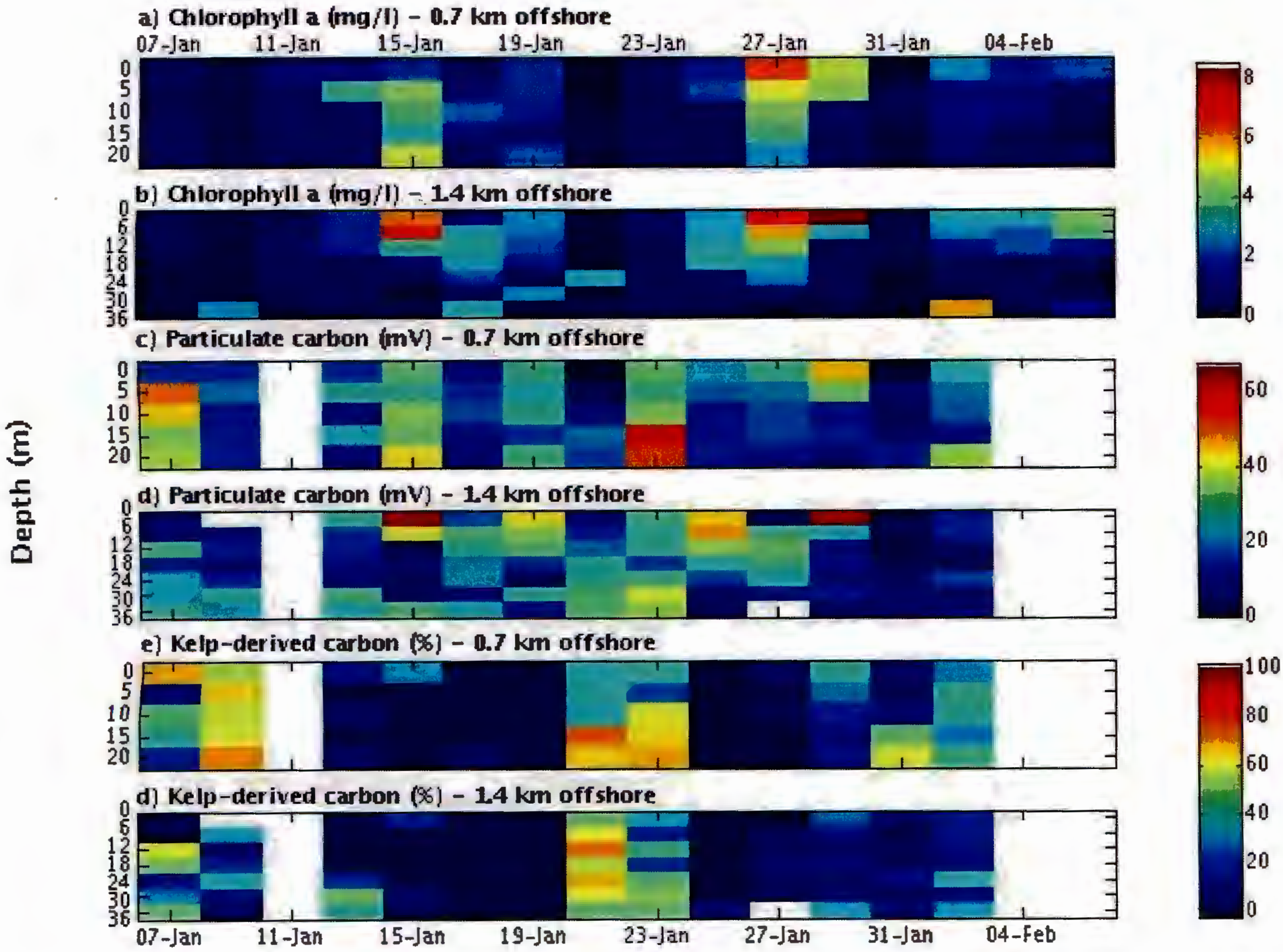

Fig. 5: Biological data for Cape Columbine. Chlorophyll *a* concentrations (mg/l) are shown for specified depth intervals for (a) the middle station and (b) the outer station. Quantity of organic carbon (mV = millivolts) is given at specified depth intervals for (c) the middle station and (d) the outer station, Percentage kelp-derived carbon of particulate organic matter is shown for specified depth intervals for (e) the middle station and (f) the outer station. High values are represented towards the red end of the spectrum and low values towards the blue end.

2007 and 22 Jan 2007. A surface peak in chlorophyll *a* concentration was recorded on 27 Jan 2007 lasting until 29 Jan 2007 followed by no chlorophyll on 31 Jan 2007. The concentration of chlorophyll *a* decreased with depth in the water column (Fig. 5a, b). Highest values were recorded on the surface at the outer station, reaching maxima of ~7 to 8 mg/*l*. Concentrations were higher offshore, ~2 to 4 mg/*l*, relative to the middle station. An isolated peak of ~6 mg/*l* was recorded at 36 m depth on 2 Feb 2007.

Quantities of organic carbon (Fig. 5c, d) were consistently high throughout the water column at the middle station during peaks on 7, 15, 19, 23 and 29 Jan 2007. The highest value (15 mV) recorded at this station was at 15 m depth on 23 Jan 2007. At the outer station, average quantities of organic carbon were highest from 6 m depth upward. Peaks at this station were detected on 15, 19, 23 – 27, and 29 Jan 2007. In general, peaks in quantity of organic carbon were recorded with simultaneous peaks in concentration of chlorophyll *a*, but with concurrent reductions in % kelp derived carbon (Fig. 5e, d).

Pulses of high percentages of kelp-derived carbon were recorded during periods when chlorophyll was lowest – a trend that was also observed at Elandsbaai, but was more apparent at Cape Columbine (Fig. 5e, d). Initially, percentages of kelp-derived carbon were high at both distances offshore throughout the entire water column on 7 Jan 2007 and 9 Jan 2007. Highest values were detected at the middle station: ~65% at 0 m and 75% at 20 m. The outer station revealed a highest value of *60% at 12* m depth on 7 Jan 2007. Extremely low percentages of kelp-derived carbon (<15 but mostly 0%) were maintained until 21 Jan 2007 when an intense yet brief two-day increase in % kelp-derived carbon was detected throughout the water column. By 25 Jan 2007, % kelp-derived carbon values had returned to trace levels of <5%. During the peak, % kelp-derived carbon ranged between ~25 and 75% at both stations throughout the water column. A final but less intense peak of % kelp-derived carbon was recorded on 29 Jan 2007 and lasted until 2 Feb 2007.

Isotopic ratios

$\delta^{13}C$ and $\delta^{15}N$ isotopic ratios of particulate organic matter (POM) samples from both study sites are shown in Fig. 6. The average enrichment of isotopic ratios obtained from Elandsbaai POM was greater than those ratios from Cape Columbine POM (Fig. 6). Isotopic ratios for POM sampled at Cape Columbine ranged between -21.49‰ and -14.6‰ for $\delta^{13}C$ and -2.04‰ to 8.75‰ for $\delta^{15}N$. Results for Elandsbaai ranged from -21.03‰ to -14.98‰ for $\delta^{13}C$ and between 3.76‰ (excluding an outlier of 1.19‰) and 8.91‰ for $\delta^{15}N$. The range in $\delta^{15}N$ isotopic ratios was greater than those of $\delta^{13}C$. Most of the $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios for POM from Elandsbaai and Cape Columbine fell between the phytoplankton and *E. maxima* reference points. A number of samples from Elandsbaai and Cape Columbine did, however, exceed the $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios of phytoplankton. Some of the samples from Cape Columbine displayed a tendency towards the $\delta^{13}C$ and $\delta^{15}N$ reference isotopic ratio of diatoms. There were no obvious differences in ratios for either $\delta^{13}C$ or $\delta^{15}N$ between samples taken at different distances offshore, at either Cape Columbine or Elandsbaai.

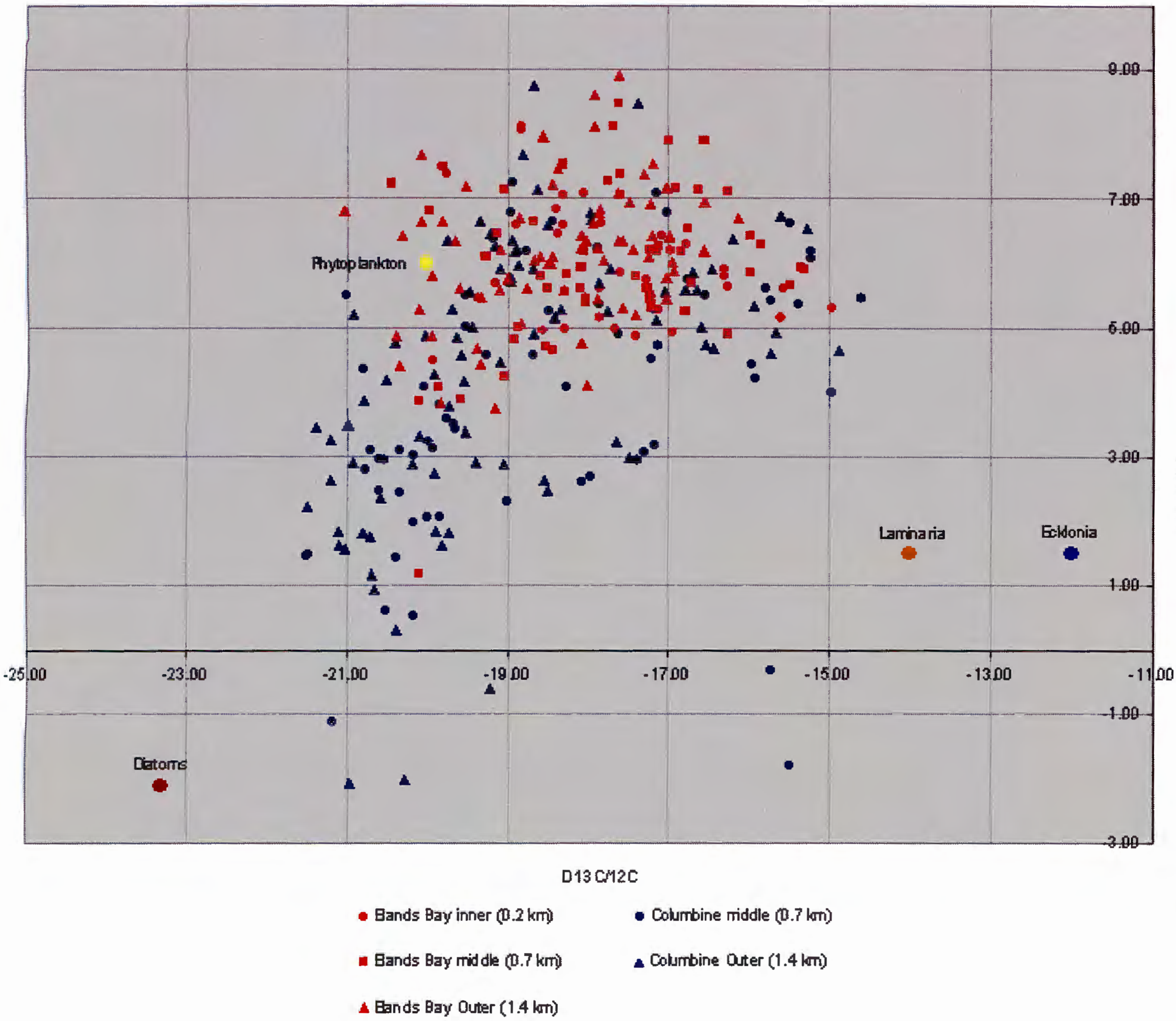

Fig. 6: $\delta^{13}C$ and $\delta^{15}N$ ratios obtained from particulate organic matter, sampled at each station throughout the water column for Cape Columbine (blue symbols) and Elandsbaai (red symbols). Different symbols have been designated for each sampling station. Reference $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios for *Ecklonia maxima, Laminaria pallida* (Bustamante and Branch 1996), Phytoplankton (Owen 1987) and diatoms (Kaehler et al. 2006) have been included.

Patterns of chlorophyll a, particulates and kelp contribution between sites and oceanographic conditions

Results from ANOVA show significant differences in concentration of chlorophyll *a*, amount of organic carbon and % kelp-derived carbon were apparent between Elandsbaai and Cape Columbine (Table 2, Fig. 7). These variables also differed significantly between oceanographic conditions (upwelling, downwelling and relaxation) within each study site. Chlorophyll *a* concentrations were significantly lower at Cape Columbine in comparison to Elandsbaai (Table 2, Fig. 7a). Results from the Tukey HSD post-hoc test show that chlorophyll *a* concentration was significantly lower during upwelling at Cape Columbine and Elandsbaai in comparison to relaxation and downwelling ($P < 0.0001$). Organic carbon at Cape Columbine was found to be significantly lower in comparison to Elandsbaai ($P < 0.0001$ – Fig. 7b). Post-hoc results revealed it did not vary with oceanographic conditions at Cape Columbine, yet but at Elandsbaai it did have significantly lower levels during upwelling at than during relaxation and downwelling.

Significant differences in % kelp-derived carbon were displayed between upwelling, downwelling and relaxation events ($P < 0.0001$). Furthermore a significant interaction was found between sites and oceanographic conditions for % kelp-derived carbon ($P < 0.0001$). One of the most significant results obtained during this study was that % kelp-derived carbon increased markedly with upwelling at Cape Columbine in comparison to lower values obtained during relaxation and downwelling events (Fig. 7c). However, at Elandsbaai no significant differences existed between upwelling, downwelling and relaxation.

Patterns of chlorophyll a, particulates and kelp contribution between distances from shore and depth layers

Comparisons of chlorophyll *a* concentration, organic carbon and % kelp-derived matter among the sampling stations at different distances offshore and depth throughout the water column are summarised in Table 2. Concentrations of chlorophyll *a* were on significantly higher in the upper layer of water across all sampling stations at Elandsbaai ($P < 0.001$ – Fig. 8a). In addition, chlorophyll *a* concentrations displayed a significant decrease with distance offshore ($P < 0.05$). A significantly greater quantity of organic carbon existed within the top layer of water across all sampling stations at Elandsbaai ($P <0.001$ – Fig. 8b). Furthermore, % kelp-

Table 2: Results obtained from fixed factor ANOVAs testing for differences in concentration of chlorophyll-a, amounts of organic carbon and percentages of kelp-derived carbon between Elandsbaai and Cape Columbine, and during different oceanographic conditions. Significant differences are printed in bold. Sites were Elandsbaai and Cape Columbine and Oceanographic conditions comprised upwelling, downwelling and relaxation.

Dependant Variable	Factor	SS	Df	MS	F	P
Chlorophyll-a	Site	5.586	1	5.586	39.91456	**0.000000**
	Oceanographic condition	12.877	2	6.43849	46.00972	**0.000000**
	Site*Oceanographic condition	0.515	2	0.25756	1.84051	0.160180
Organic carbon	Site	10.1708	1	10.1708	142.761	**0.000000**
	Oceanographic condition	1.0098	2	0.5049	7.087	**0.000982**
	Site*Oceanographic condition	0.1956	2	0.0978	1.373	0.255019
% Kelp C	Site	14356.2	1	14356.2	53.3985	**0.000000**
	Oceanographic condition	21266.8	2	10633.4	39.5516	**0.000000**
	Site*Oceanographic condition	11404.4	2	5702.2	21.2095	**0.000000**

derived carbon displayed a similar distribution to that of chlorophyll *a* concentration decreasing with distances offshore ($P < 0.05$ – Fig. 8c). However, with regard to % kelp-derived carbon, post-hoc results do not reveal any significant differences between sampling stations and depth.

At Cape Columbine, chlorophyll *a* concentrations accorded with the results obtained for Elandsbaai. More chlorophyll *a* was found in the top layer of water throughout the water column ($P < 0.0001$ – Fig. 9a). However, quantities of organic carbon and % kelp-derived carbon did not differ significantly among different distances offshore or among different depths at Cape Columbine (Fig. 9b, c).

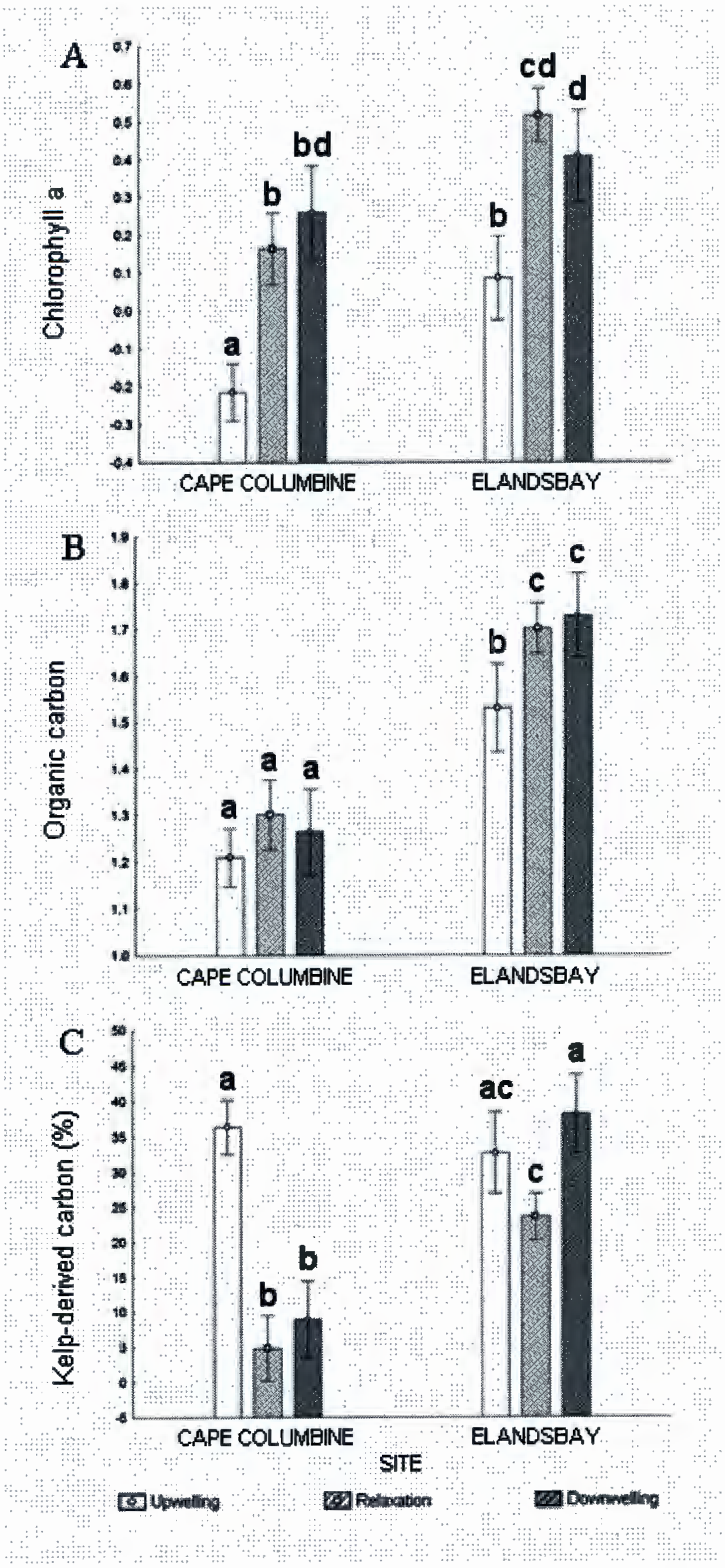

Figure 7: Mean (± 95% CI) values for (A) concentration of chlorophyll-a, (B) amounts of organic carbon (mV) and (C) percentages of kelp-derived carbon between the study sites Elandsbaai and Cape Columbine and in relation to upwelling, downwelling and relaxation. Significant differences are represented with a different letter above each bar (Tukey post-hoc tests, $P < 0.05$).

Table 3: Results obtained from fixed-factor ANOVAs testing for differences in concentration of chlorophyll *a*, amounts of organic carbon and percentages of kelp-derived carbon between sampling stations and relative to depth within each study site. Significant differences are printed in bold. Distances offshore for Elandsbaai were inner, middle and outer and for Cape Columbine distances offshore included middle and outer. Depths are top and bottom (Table 1).

Site	Dependant Variable	Factor	SS	Df	MS	F	P
Elandsbaai	**log(Chlorophyll-a)**	Distance offshore	1.26769	2	0.63384	3.9977	**0.02001**
		Depth	1.92734	1	1.92734	12.1559	**0.00061**
		Distance offshore*Depth	0.13300	2	0.06650	0.4194	0.65807
	Organic carbon	Distance offshore	0.2934	2	0.1467	2.610	0.07684
		Depth	0.8082	1	0.8082	14.376	**0.00021**
		Distance offshore*Depth	0.0640	2	0.0320	0.569	0.56703
	% Kelp C	Distance offshore	2130.2	2	1065.1	3.6867	**0.02732**
		Depth	105.0	1	105.0	0.3634	0.54749
		Distance offshore*Depth	147.2	2	73.6	0.2547	0.77544
Cape Columbine	**log(Chlorophyll-a)**	Distance offshore	0.00872	1	0.00871	0.05689	0.81174
		Depth	3.27376	1	3.27376	21.3630	**0.00000**
		Distance offshore*Depth	0.56246	1	0.56246	3.67036	0.05690
	log(Area C) (mV)	Distance offshore	0.1463	1	0.1463	1.761	0.18651
		Depth	0.0196	1	0.0196	0.236	0.62763
		Distance offshore*Depth	0.0293	1	0.0293	0.353	0.55357
	% Kelp C	Distance offshore	1059.03	1	1059.03	2.1227	0.14726
		Depth	625.35	1	625.35	1.2534	0.26472
		Distance offshore*Depth	0.07	1	0.07	0.0001	0.99075

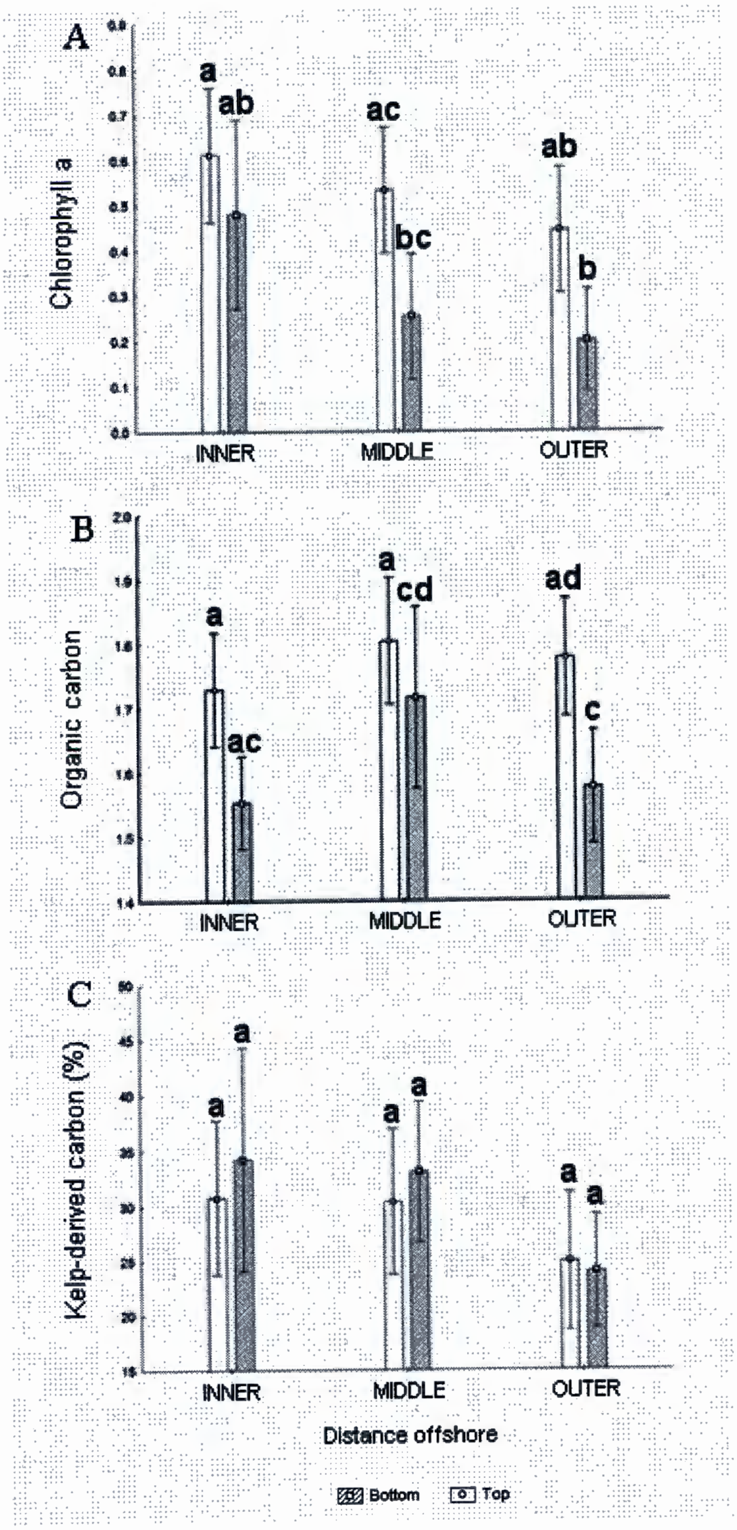

Figure 8: Mean (± 95% CI) values for (A) concentration of chlorophyll *a*, (B) amounts of organic carbon (mV) and (C) percentages of kelp-derived carbon between sampling stations and relative to depth at Elandsbaai. Significant differences are represented with a different letter above each bar (Tukey post-hoc tests, $P < 0.05$).

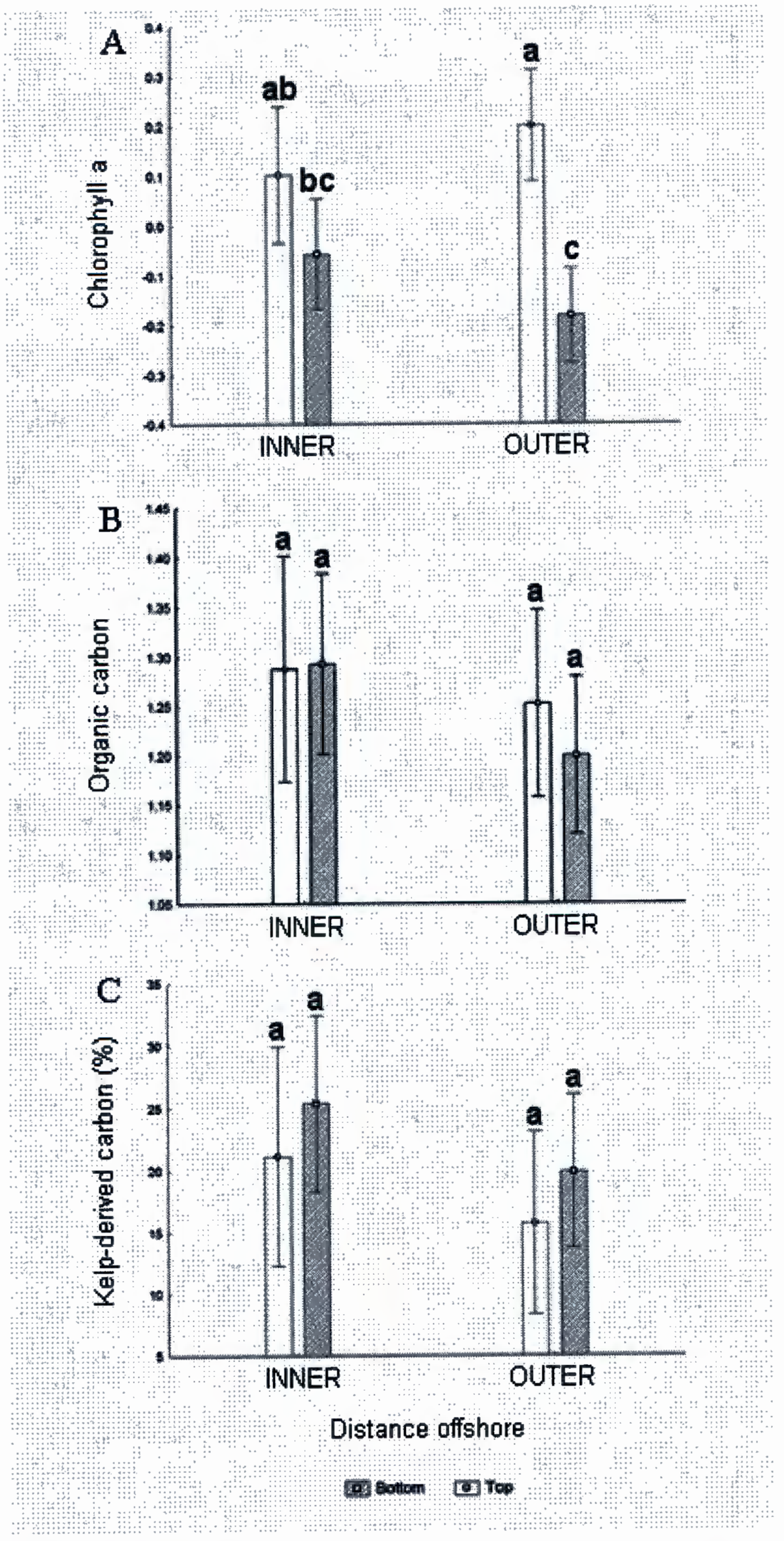

Figure 9: Mean (± 95% CI) values for (A) concentration of chlorophyll *a*, (B) amounts of organic carbon (mV) and (C) percentages of kelp-derived carbon between sampling stations and relative to depth at Cape Columbine. Significant differences are represented with a different letter above each bar (Tukey post-hoc tests, $P < 0.05$).

DISCUSSION

The results of this study clearly show that oceanographic conditionses such as upwelling, downwelling and relaxation play an important role in the productivity and transport of POM. This conforms to the findings of previous studies (Olivieri and Hutchings 1987, Fielding and Davis 1989, Painting et al. 1993). The two study sites, Elandsbaai and Cape Columbine, differed significantly with regard to quantity and composition of POM. On average, greater quantities of chlorophyll *a* (i.e. phytoplankton), organic carbon and % kelp-derived carbon were found at Elandsbaai than at Cape Columbine. These trends were explicable in terms of the different prevailing oceanographic conditionses operating at each site. Wind data, temperature at different depths, and current data, clearly illustrated episodes of upwelling, downwelling and relaxation at Cape Columbine and Elandsbaai. Cooler averages and severe drops in temperature during upwelling at Cape Columbine are typical features in agreement with previous findings (Andrews and Hutchings 1980) that have defined this headland as an upwelling center. The magnitude and extent of northward/offshore currents during such periods, further demonstrates this point. Elandsbaai, by contrast, displayed episodes of intense stratification and somewhat higher average temperatures throughout the water column, indicating that it is a retention zone lying within an upwelling shadow as described by Monteiro and Roychoudhury (2005). Above all, downwelling occurred at this site when complete southward reversals in wind and current direction were observed, with simultaneous elevation of temperature throughout the water column. Concurrently, a relatively smaller peak in temperature was detected at Cape Columbine, but insignificant reversal in current direction confirmed suspicions of weaker downwelling potential at this site.

Profound differences in biological variables between Elandsbaai and Cape Columbine reiterate the contrasting oceanographic conditions observed between these sites. These obviously have implications with regard to the supply of food. Upwelling at Cape Columbine was conducive to low amounts of chlorophyll *a* and organic carbon, but significantly elevated levels of % kelp-derived carbon were recorded in comparison to periods of relaxation and downwelling. Similar results were found at Elandsbaai with significantly lower amounts of chlorophyll *a* and organic carbon during upwelling. Levels of % kelp-derived carbon did not differ significantly between oceanographic conditions at Elandsbaai. Periods of relaxation at Cape

Columbine had similarly high amounts of chlorophyll *a* but low amounts of organic carbon and % kelp-derived carbon in comparison to downwelling. At Elandsbaai, relaxation resulted in the highest average chlorophyll *a* and organic carbon readings obtained during the study. Both showed similarly high readings of chlorophyll *a* and organic carbon during relaxation and downwelling. However, significantly lower amounts of % kelp-derived carbon were recorded during relaxation episodes at Elandsbaai.

Interestingly, the average contribution of kelp-derived matter found during this study reached a maximum of 36% (during upwelling at Cape Columbine). This contradicts the findings of Bustamante and Branch (1996), who report that kelp detritus constituted the greater proportion of particles, accounting on average for more than 70% of all POM, regardless of exposure or tidal period. Based on the findings of this study, it is quite clear that kelp-derived POM is contributing a significantly lower amount of particulate food than expected. On average higher amounts of chlorophyll *a* were found in the surface layers of the water column at both Cape Columbine and Elandsbaai. Apart from this, no stratification of POM was observed throughout the water column and no significant differences in amount of POM were found between the different distances of sampling stations offshore.

During active upwelling, currents in the water column move in an offshore direction at the surface (Ekman layer) and onshore at the bottom. This process has been shown to be of greatest intensity at headlands, such as Cape Columbine, yet is significantly reduced leeward of such topography, particularly in embayments (Andrews and Hutchings 1980). The overriding Benguela current, in combination with persistent upwelling winds from the south, pushes upwelled water from Cape Columbine northward towards St. Helena Bay and Elandsbaai where it retentively circulates and matures (Monteiro and Roychoudhury 2005). Newly upwelled water is characteristically clear with low concentrations of phytoplankton and detritus (Andrews and Hutchings 1980, Olivieri 1983). My results conform to such findings, as low chlorophyll *a* values were recorded during upwelling at both sites. This can be attributed to the time-lag in response of phytoplankton to the sudden increase in available nutrients from newly upwelled water. In turn, this would explain the higher chlorophyll *a* concentrations observed in the mature upwelled water characteristic to Elandsbaai and St. Helena Bay. The notion that low amounts of detritus are associated with upwelling (Andrews and Hutchings 1980, Olivieri 1983) is not supported by the amount of kelp-derived matter recorded at Cape Columbine during such events. Furthermore, the increase in % kelp-derived matter during upwelling was not simply the result in low levels of phytoplankton but rather due to an actual increase in quantity of kelp-derived matter throughout the water column. The most plausible explanation for this is the likely stirring up and surface transport of benthic kelp-derived matter by nearshore upwelling currents. It can be assumed that with continued upwelling the supply of kelp-derived matter would soon be exhausted and transported northward and offshore, thus depriving coastal communities of a potentially valuable food source. However, in the event of a brief upwelling pulses that are followed by relaxation and subsequent onshore wash-up, this kelp-derived matter could remain in the nearshore zone within reach of coastal filter feeders, hence serving as a supplementary food source in the absence of phytoplankton.

Following a reduction in northward winds, upwelling processes come to a halt and the water column stabilises as a result of being warmed by the sun, giving rise to relaxation (Painting et al. 1993). In absence of further disturbance, the water column becomes well stratified with the development of a thermocline, separating the upper warm layer of water from the cooler dense layer at the bottom. This relaxation, coupled with retention of matured upwelled water, would account for the extremely high chlorophyll *a* levels recorded at the surface of the water column in Elandsbaai. Comparatively lower concentrations of chlorophyll *a* detected at Cape Columbine during relaxation could be explained by the absence of retention and frequent disturbances throughout the water column. Temperature profiles between the two study sites (Figs. 2b and 4b) show that a greater frequency in upwelling pulses occurred at Cape Columbine, thus supporting the notion of a frequently disturbed water column, and hence reduced levels in phytoplankton productivity. This is supported by previous studies which correlate phytoplankton blooms with mature upwelled water subjected to relaxation and retention in bays (Painting et al. 1993). In addition, previous studies have shown that the early stages of phytoplankton blooms (in relatively newly upwelled water) largely consist of diatoms, which are succeeded by dinoflagellates as the water mass matures and becomes depleted in available nitrogen (Painting et al. 1993, Olivieri and Hutchings 1987). According to kinetic fractionation (Fry 2006), dinoflagellates, being the later successional species, would be expected to display enrichment of the heavier ^{13}C and ^{15}N isotopes in comparison to preceding diatoms. Hence diatoms would be expected to populate newly upwelled water in the vicinity of Cape Columbine and dinoflagellates the older, mature water retained during relaxation at Elandsbaai. This appears to be the case as average enrichment of POM with heavier isotopes was observed at Elandsbaai in comparison to Cape Columbine, which showed an average tendency towards lighter isotopic fractionation (Fig. 6). Based on these results, the take-home message is that a greater amount of food is available at Elandsbaai, in the form of phytoplankton, in comparison to Cape Columbine. The driving factor behind this deduction is that oceanographic conditions at Elandsbaai are conducive to higher production levels of phytoplankton which is retained within a bay, therefore allowing consumers to exploit this readily available source of particulate food. In contrast, frequent disturbance of the water column at Cape Columbine results in the net exportation of nutrients and food, thus preventing the opportunity for a significant phytoplankton bloom to take place.

With southward/onshore reversal in wind direction and subsequent downwelling, during which the Ekman layer moves onshore and the bottom layer of water offshore, increased amounts of chlorophyll *a* were observed at Cape Columbine which were similar to those recorded during downwelling at Elandsbaai. With persistent southward wind, southward downwelling currents essentially flushed the phytoplankton-rich water out of Elandsbaai and St. Helena Bay around the headland, towards Cape Columbine. This probably explains the increased chlorophyll *a* concentrations present during downwelling at Cape Columbine. However, it should be noted that this concentration of chlorophyll *a* was not significantly different to that recorded during episodes of relaxation. It is likely that during downwelling, most phytoplankton is driven downward and offshore by subsurface currents by the time it reaches Cape Columbine, possibly explaining this anomaly. Similar observations are evident from the results obtained at Elandsbaai and it is likely that the same explanation applies. Downwelling at Elandsbaai did, however, contribute to a significant increase in % kelp-derived carbon in comparison to relaxation episodes, hence supplementing the coastal community with an additional source of food. Levels of % kelp-derived carbon were, on the other hand, significantly lower at Cape Columbine during downwelling in comparison to that supplied by upwelling episodes. Therefore as a supply mechanism of food, downwelling does provide an increase in kelp particulate matter to retentative bays but apart from that, no significant contribution was made by downwelling (in comparison to relaxation) to the overall availability of POM as a food source. If anything, it deprived coastal waters at Cape Columbine of suspended particulate food, contrary to expectations.

Surprisingly, no significant stratification of POM was observed throughout the water column for sampling stations at Cape Columbine and Elandsbaai, apart from the expected surface peaks of chlorophyll *a*. In addition, there was a similar lack of significant differences in quantities of POM at stations sampled at different distances offshore. Perhaps the relatively close proximity and shallow depth of sampling stations accounts for this, as I would expect nearshore turbulence and oceanographic conditionses to influence the entire water column.

Conclusions

The two study sites, with contrasting wave-exposure and surrounding topography, display significant differences in prevailing oceanographic conditions. Oceanographic conditionses clearly influenced the rate, composition and amount of food supplied to coastal consumers. Upwelling can be regarded as a transport mechanism for the import of kelp-derived particulates at coastal upwelling centers, given that upwelling episodes are brief and followed by a period of relaxation, thus avoiding major offshore advection of upwelled kelp matter. Relaxation, a process most pronounced at Elandsbaai, primarily serves as a mechanism for building food reserves, mainly consisting of phytoplankton, which are retained and later distributed to neighbouring southward coastlines such as Cape Columbine during episodes of downwelling. Although this phytoplankton-rich food source is evacuated from retentative bays, it is substituted by increases in kelp-derived matter which provide temporary nourishment for the coastal community.

In conclusion, oceanographic conditionses play a key role in providing coastal consumers with food in the form of POM. This food primarily consists of phytoplankton, as indicated by relatively low percentage contribution of kelp-derived matter to overall quantities of POM. This could be a seasonal trend, and perhaps during the months of winter when phytoplankton productivity is at a minimum, kelp-derived matter may constitute the primary food source. With heavier seas and rough conditions during the winter months, it is likely that more kelp enters the detrital food web through increased abrasion, thus potentially filling the role as a source of food for coastal consumers. Additional research throughout all seasons of the year and at greater spatial scales should provide further insight behind the driving mechanisms regarding transport, composition and rate at which particulate food is supplied to the coastal community.

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1. I know that plagiarism is wrong. Plagiarism is to use another's work and to pretend that it is one's own.
2. Each significant contribution to, and quotation in, this project from another source has been attributed, cited and referenced.
3. This project is my own work
4. I have not allowed and will not allow anyone to copy my work with the intension of passing it off as his/her own.

Signature: ______________________